

Morphological organization of the male palpal organ in Australian ground spiders of the genera *Anzacia*, *Intruda*, *Zelanda*, and *Encoptarthria* (Araneae: Gnaphosidae)

Boris P. Zakharov: Department of Natural Sciences, La Guardia Community College of the City University of New York, 31-10 Thomson Avenue, New York, New York 11101, USA

Vladimir I. Ovtcharenko¹: Department of Natural Sciences, Hostos Community College of the City University of New York, 500 Grand Concourse, New York, New York 10451, USA

Abstract. Detailed morphologies of the male copulatory organs of the Australian genera *Anzacia*, *Intruda*, *Encoptarthria* and *Zelanda* and the Holarctic genus *Drassodes* are presented. The homology of several palpal elements within the family Gnaphosidae is established. The possible homology of these structures with those in other spider families is discussed. The ground plan of the gnaphosoid genital bulb is compared with the bulb of other Entelegynae genera. Australasian spider genera have a peculiar organization of the male palpal organs. Thus, the Holarctic genus *Drassodes* was also analyzed for comparison. The analysis of the male copulatory organs is presented and its implication for classification of these groups is discussed. The taxonomic changes we make here are the transfer of four species from the genus *Megamyrmaekion* to genus *Encoptarthria*: *E. echemophthalma* (Simon 1908), *E. penicillata* (Simon 1908), *E. perpusilla* (Simon 1908), and *E. vestigator* (Simon 1908). One species is transferred from genus *Echemus* to genus *Encoptarthria*: *E. grisea* (L. Koch 1873). New synonymy established: *Encoptarthria echemophthalmum* (Simon 1908) = *Encoptarthria serventyi* Main 1954, syn. n.

Keywords: Taxonomic changes, *Drassodes*, *Megamyrmaekion*, *Encoptarthria serventyi*

The copulatory organs of male spiders are unique in the animal kingdom. They do not have a direct connection with the testes and are located at the distal segment of the male pedipalps. The internal sexual organs, the testes, lie as paired structures inside the abdomen (Foelix 1996). Sperm is released through the ventral genital opening of the deferential ducts in the epigastric furrow. The male exudes the sperm through this opening onto a special sperm web. From here, it is collected into the fundus of the copulatory organ (Foelix 1996). The sperm duct is a long, coiled tube that folds into a complex morphological structure, the genital bulb. The genital bulb is composed of inflatable membranes (hematodochae) and a set of sclerites (subtegulum, tegulum, and embolus). Usually it also bears additional accessory structures: projections and apophyses.

During copulation, the male transfers seminal fluid via the embolus into the female copulatory duct. It is widely accepted that the male palp fits specifically into the female epigynum of conspecifics. This assumption underlies the importance of male and female genitalia in species identification, since it was first used for this purpose (Westring 1861; Menge 1843, 1866; Wagner 1887; Comstock 1910, 1920). Every article or monograph on ground spider taxonomy includes illustrations of male and female copulatory organs. The structure of the genital bulb has been analyzed for some groups of gnaphosids (Miller 1967; Platnick & Shadab 1983), and some primary homologous structures have been established. Senglet (2004) made a detailed analysis of the basic ground plan of the palp of zelotines. Our recent study of the Australian genus *Encoptarthria* Main 1954 shows that the bulb of these spiders is significantly more complex than in other gnaphosids. The embolar part of the bulb of *Encoptarthria* has a set of structures that are lacking in other ground spiders. However, these structures play an important role in *Encoptarthria* species identification. Observation of other

encoptarthrein spiders shows that they have a remarkably complex palp organization and many structures that require standardized labeling. The most characteristic part of these spiders' male bulb is the apical division. This part of the male bulb is especially complex and has sclerites that are lacking in the bulbs of other gnaphosids. It is, therefore, necessary to examine and label the male copulatory organs to understand homologous structures and, hence, relations of the genus *Encoptarthria* with other ground spiders.

METHODS

Genital bulbs of the following species were studied: *Anzacia gemma* (Dalmás 1919) [New Zealand: Kaikoura, January 1961, collector unknown; Zoology Department, University of Canterbury]; *Drassodes lapidosus* (Walckenaer 1802) [Azerbaijan: Pirkulinsky Natural Reserve, elev. 1300 m, 31 May 1984, coll. D. Logunov; V. Ovtcharenko collection]; *Encoptarthria echemophthalma* (Simon 1908) [Western Australia: Jandkott Airport, 32°05'31"S, 115°52'28"E, wet pitfalls, 1 September–4 November 1994, coll. J.M. Waldock, A.F. Longbottom; Western Australian Museum, T50511]; *Encoptarthria grisea* (L. Koch 1873) [Tasmania: Lutana Risdon Rise, 5 May 1929, coll. V.V. Hickman; Australian Museum, KS 32434]; *Encoptarthria penicillata* (Simon 1908) [Western Australia: Goldfields Survey, Yundamindra, 29°23'S, 122°28'E, mulga/shrubs, July 1981, coll. W. F. Humphreys et al.; Western Australian Museum, T50280]; *Intruda signata* (Hogg 1900) [New Zealand: Titirangi, January 1965; Australian Museum, KS 31611]; *Zelanda erebus* (L. Koch 1873) [New Zealand: Christchurch, September 1989, collector unknown, Florida State Collection of Arthropods].

Taxonomic changes.—Our research of Australian Gnaphosidae (manuscript in preparation) shows that some taxa are misplaced. Based on the structure of the copulatory organs, shape and position of the eyes and structure of the spinnerets, four species are transferred from the genus *Megamyrmaekion* Reuss 1834 to the genus *Encoptarthria*: *E. echemophthalma*

¹Corresponding author. E-mail: vio@hostos.cuny.edu

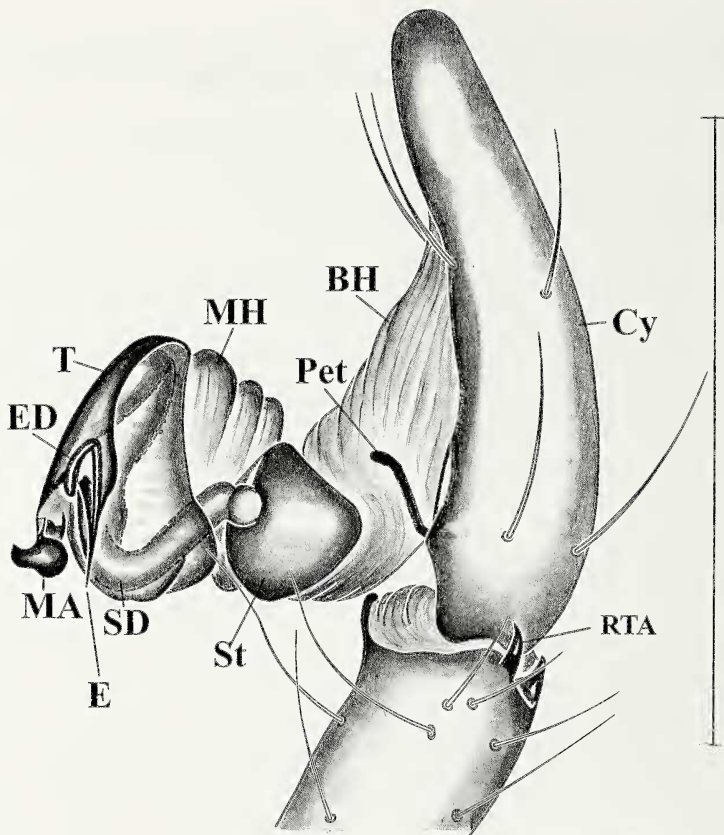


Figure 1.—*Drassochus lapidosus*, left palp, lateral view. BH - basal hematodocha; Cy - cymbium; E - embolus; ED - ejaculatory duct; MA - median apophysis; MH - median hematodocha; Pet - petioles; RTA - retrolateral tibial apophysis; SD - sperm duct; St - subtegulum; T - tegulum.

(Simon 1908), *E. penicillata* (Simon 1908), *E. perpusilla* (Simon 1908), and *E. vestigator* (Simon 1908), and one species is transferred from the genus *Echemus* Simon 1878 to the genus *Encoptarthria*: *Encoptarthria grisea* (L. Koch 1873). One name is synonymized: *Encoptarthria echemophthalmum* (Simon 1908) = *Encoptarthria serventyi* Main 1954, syn. n.

Expansion of genital bulbs.—The left palps were detached and submerged overnight in a weak, watery solution of potassium hydroxide (KOH) at room temperature. This allowed the bulb to expand. The bulb was then transferred to distilled water, where expansion continued. All bulb dissections were preserved in 75% alcohol. Illustrations were made with the aid of a dissecting microscope (Nikon SMZ-U). Drawings were scanned and corrected using Photoshop software.

Homology.—To determine the homologous structures of the bulb, we used the following classical and widely applied

criteria: 1) structure position; 2) morphological similarity with other known structures and 3) correspondence of the structure with other characters (Remane 1952; Patterson 1982; Sierwald 1990; Coddington 1990).

Terminology.—It is generally accepted that the tripartite genital bulb in male spiders is plesiomorphic (Platnick & Gertsch 1976; Kraus 1978; Haupt 1983; Sierwald 1990). The present study supports the conclusion that large sclerites (subtegulum and tegulum) are homologous in all spiders. These sclerites are organized around the opening on one side and are blindly closed on the other side tube that serves as a temporary sperm reservoir. Before mating, males fill their palps with sperm, and sperm is stored there until mating occurs. The tube has an enlarged, closed end (the fundus), a long coiled tube (the sperm duct), and a narrow tube with an opening at the end (ejaculatory duct). The ejaculatory duct has

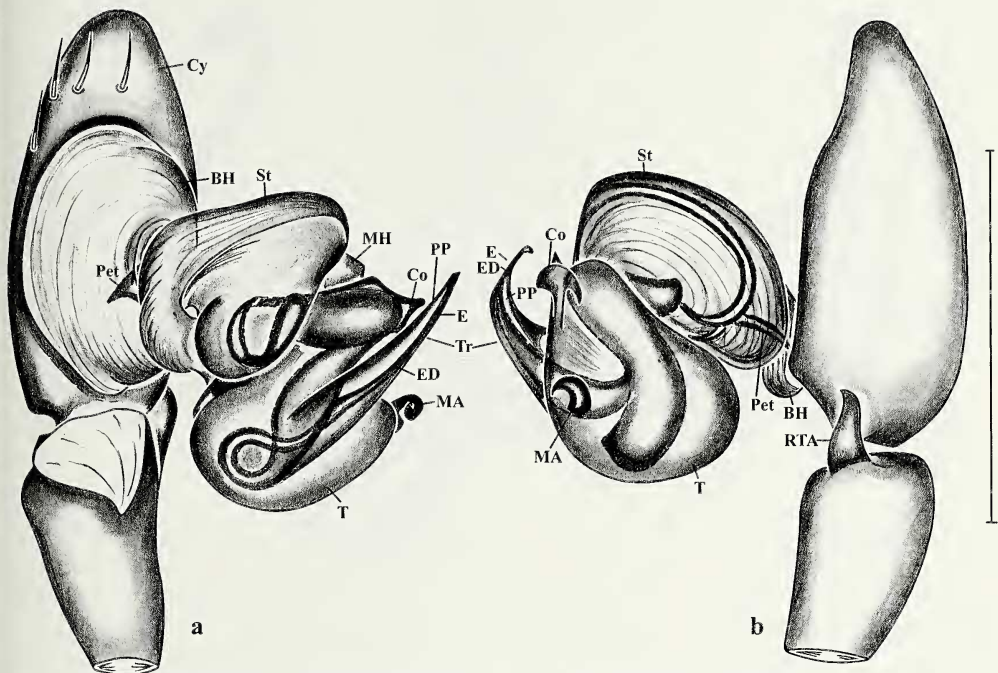


Figure 2.—*Intruda signata*, left palp. a. Ventral view; b. Dorsal view. BH – basal hematodocha; Co – conductor; Cy – cymbium; E – embolus; ED – ejaculatory duct; MA – median apophysis; MH – median hematodocha; Pet – petioles; PP – pars pendulum of embolus; RTA – retrolateral tibial apophysis; SD – sperm duct; St – subtegulum; T – tegulum; Tr – truncus of embolus.

an opening from which sperm is ejected into the female receptaculum seminis during copulation.

The sperm duct begins at the fundus and, in this study all structures that occupy a nearby position are considered proximal. All structures that are near the ejaculatory duct are considered distal. Structures near the alveolus of the cymbium in the unexpanded bulb are dorsal. Parts that occupy a ventral position are usually easily visible on the ventral side of the unexpanded bulb.

The median apophysis and conductor refer to the tegular apophyses. The conductor is an inflatable membranous projection on the upper surface of the first half of the tegulum. It is an outgrowth of the membranous walls of the tegulum. The tip of the conductor locates close to the embolus. The median apophysis is a heavily sclerotized structure that occupies a position distal from the conductor on the tegulum. It is connected to the tegulum via an inflatable membrane and is not directly associated with the embolus.

The term distal sclerotized tube was introduced by Sierwald (1990), who gave this name for the identification of a tubular sclerotized structure that occupies the position between the tegulum and embolus and is connected to both structures by inflatable membranes. The distal sclerotized tube is a part of the apical bulb division. The apical bulb division is identified

by the constriction of the sperm duct and its transformation into a narrow ejaculatory duct. This constriction of the sperm duct into the ejaculatory duct on the border between the distal part of tegulum and distal sclerotized tube is associated with the apical (embolar) bulb division. Sierwald's (1990) observations of the distal sclerotized tube was carried out on pisaurids. We use the distal sclerotized tube term here in the description of the gnaphosid's male bulb. However, the similar position and morphology of these sclerites in pisaurid and gnaphosid spiders does not imply their homology.

The distal apophysis is anchored via a membranous connection to the tegulum and simultaneously to the distal sclerotized tube. Thus, it attaches to both the middle and apical divisions of the genital bulb. The terminal and subterminal apophyses are structures of the apical division of the bulb. It is not clear whether these structures are homologous among gnaphosid spiders.

Senglet (2004) made a detailed study of the male palps of the genera *Zelotes* Gistel 1848, *Drassyllus* Chamberlin 1922 and *Trachyzelotes* Lohmander 1944. However, his usage of the various terms in some cases is questionable. Therefore, authors typically follow Sierwald's (1990) approach in labeling palp structures. Sierwald (1990) deliberately analyzed terms used in describing the male palps of pisaurid spiders. Her

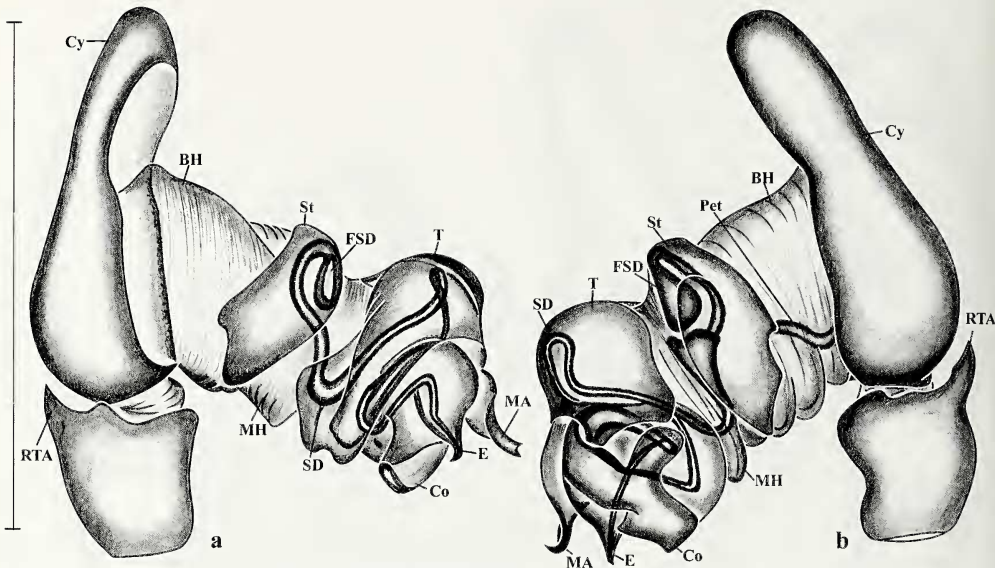


Figure 3.—*Anzacia gemmea*, left palp. a. Lateral view; b. Retrolateral view. BH – basal hematodocha; Co – conductor; Cy – cymbium; E – embolus; FSD – fundus of sperm duct; MA – median apophysis; MH – median hematodocha; Pet – petioles; RTA – retrolateral tibial apophysis; SD – sperm duct; St – subtegulum; T – tegulum.

analysis is consistent, systemic and leans on the classical definition of homology (Remane 1952; Patterson 1982).

Abbreviations used.—BH – basal hematodocha; Co – conductor, Cy – cymbium, DA – Distal apophysis, DCL – distal conductor lobe, DST – distal sclerotized tube, DTM – distal tubular membrane, DTP – distal tegular projection, E – embolus, ED – ejaculatory duct, F – fulcrum, FSD – fundus of sperm duct, LA – lateral apophysis, LSA – lateral subterminal apophysis, MA – median apophysis, MCL – median conductor lobe, MH – median hematodocha, PCL – proximal conductor lobe, Pet – petioles, RTA – retrolateral tibial apophysis, SD – sperm duct, St – subtegulum, STA – subterminal apophysis, T – tegulum, TA – terminal apophysis, TM – terminal membrane.

RESULTS

Drassodes lapidosus (Walckenaer 1802) (Fig. 1) has a small and simple sharply pointed retrolateral tibial apophysis. The basal and median hematodochae are well developed and are clearly visible in an expanded palp. The subtegulum and tegulum are open spirals, not a closed ring, with a single loop. The conductor is a small membrane, weakly developed. The median apophysis has a heavily sclerotized tip in the shape of an eagle's beak and sits on the inflatable membrane. The apical division of the bulb has only the embolus. The embolus is comparatively short and barb-like. It is firmly and broadly attached to the distal part of the tegulum. The embolus of *Drassodes* appears to consist of only the truncus. The pars pendula is not developed.

Intruda signata (Hogg 1900) (Fig. 2) also has a small and simple-shaped retrolateral tibial apophysis. The basal and median hematodochae are visible and well developed. The subtegulum and tegulum are open spirals with a single loop. The conductor is well developed, with a membranous base and partially sclerotized tip that is divided into two lobes at the top. The embolus is a big strong spine, slightly curved. Walls of the convex side of embolus are heavily sclerotized and called the truncus. The concave side of the embolus is covered by an expandable membrane called the pars pendulum. The tip of the embolus in an unexpanded bulb rests in a groove between two lobes of the conductor. The median apophysis, which in all gnaphosid spiders is distal to the conductor on the tegulum, is a strong sclerotized hook that rests on an inflatable membranous base.

In general, the bulb construction of *Intruda signata* is very similar with that of *Drassodes lapidosus*. The difference between these two bulb types is the more complicated construction of the conductor and embolus in *Intruda signata*.

Anzacia gemmea (Dalmis 1919) (Fig. 3) has a palp similar to those of *Drassodes* and *Intruda*. It consists of the basal and median hematodochae, and the subtegulum and tegulum sclerites. The tegulum is armored with the conductor and median apophysis. The embolus, as in the two species above, is fused with the tegulum and immovable. The most specific characteristic of the male *Anzacia* palp is the special shape of conductor. It is a sclerotized structure subdivided into three lobes, which gives it the appearance of a cloverleaf.

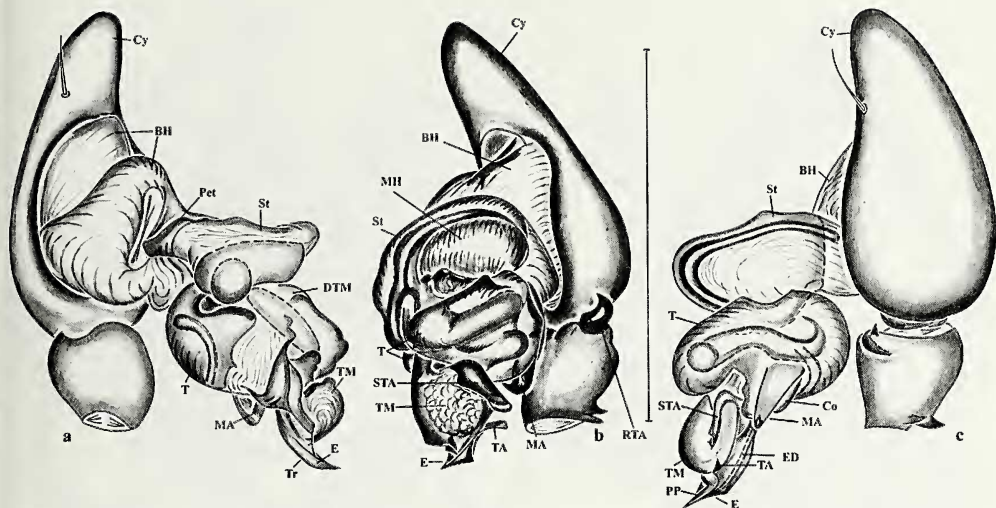


Figure 4.—*Zelanda erebus*, left palp. a. Lateral view; b. Retrolateral view; c. Dorsal view. BH – basal hematodocha; Co – conductor; Cy – cymbium; DTM – distal tubular membrane; E – embolus; ED – ejaculatory duct; MA – median apophysis; MH – median hematodocha; Pet – petioles; PP – pars pendulum of embolus; RTA – retrolateral tibial apophysis; St – subtegulum; STA – subterminal apophysis; T – tegulum; TA – terminal apophysis; TM – terminal membrane; Tr – truncus of embolus.

Zelanda erebus (L. Koch 1873) (Fig. 4) has a retrolateral tibial apophysis that is a simple hooked structure. The basal and median hematodochae are well developed. The subtegulum and tegulum are open spirals with a single loop. The distal portion of the tegulum overlaps slightly with the proximal part and creates a weakly pronounced distal tegular projection. The median apophysis is a strong, well-developed hook-shaped sclerite. It rests on a membranous structure, which is a projection of the membranous wall of the tegulum. The conductor is an inflatable membrane, the tip of which is closely associated with a comparatively short, boat-like shaped, laminar embolus. Next to the embolus, there is a spoon-shaped terminal apophysis and a ventrally grooved subterminal apophysis. The distal part of the embolus bears a membrane that is associated with the embolus. Very probably, this membrane plays a supporting role during copulation. Comstock (1910, 1920) called this structure the “distal hematodocha.” However, because his use of the term sometimes referred to the membrane between the middle and apical divisions of the bulb and in other cases referred to part of the apical division only (Comstock 1910, 1920), we avoid using this term. Instead, the extreme distal position of the membrane and its definite association with the tip of embolus suggests a more suitable terminology of “terminal membrane”.

The retrolateral tibial apophysis of *Ecoptarthria echemophthalma* (Simon 1908) (Fig. 5) has a very complex and variable shape and may be used for species identification. It is almost as long as the cymbium and has a sharp tip. The RTA is covered by massive heavily sclerotized dents that vary in number. The RTA lies in the groove on the dorsal side of the cymbium. The dents of the RTA cling to the brim of the dorsal

cymbium's groove. This unique connection between the tibia and cymbium suggests that the RTA acts as an internal locking mechanism designed to prevent free rotation of the cymbium during copulation, similar to that observed in Theridiidae and Linyphiidae by Heimer (1982) and in *Dolomedes tenebrosus* Hentz 1844 by Sierwald & Coddington (1988). The basal and median hematodochae are well developed as in the previous species. The conductor is a membranous inflatable sack. The median apophysis is a comparatively big hook with a dent on its concave side. The tegulum is a single coiled spiral sclerite. Its distal end overlaps with its proximal part and creates a very distinct distal tegular projection that forms a characteristic hump on the unexpanded bulb. The organization of the apical division of the bulb is significantly more complex than in all the previously studied spiders. It consists of a distal sclerotized tube, embolus and group of accessory sclerites. The distal sclerotized tube is a massive, heavily sclerotized tubular structure that is connected with the distal end of the tegulum through the distal tubular membrane. At the border between the tegulum and the distal sclerotized tube, the sperm duct is significantly narrower and transforms into the ejaculatory duct. The ejaculatory duct passes through the distal tubular membrane to the distal sclerotized tube and extends from here into the embolus. On the lateral side of the distal sclerotized tube is the lateral subterminal apophysis, and on its tip is the terminal apophysis. The fulcrum is a moveable structure that is partially membranous and partially sclerotized. It rests on the very tip of the apical division of the bulb that encloses some of the proximal part of the embolus. It very likely acts as a protective sheath.

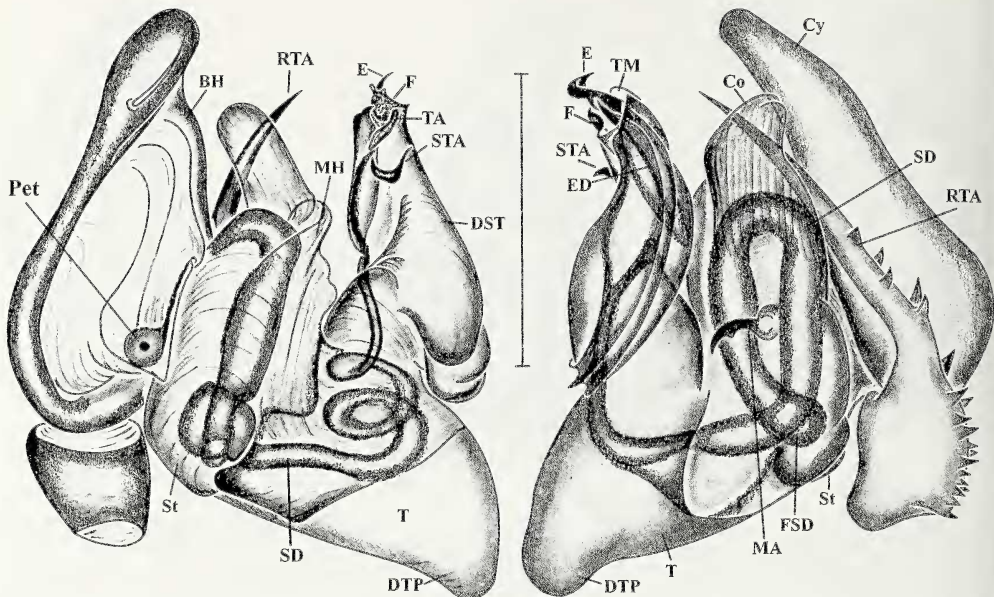


Figure 5.—*Eocoptarthria echemophthalma*, left palp. a. Lateral view; b. Retrolateral view. BH – basal hematodocha; Co – conductor; Cy – cymbium; DTP – distal tegular projection; DST – distal sclerotized tube; E – embolus; ED – ejaculatory duct; F – fulcrum; FSD – fundus of sperm duct; MA – median apophysis; MH – median hematodocha; Pet – petioles; RTA – retrolateral tibial apophysis; SD – sperm duct; St – subtegulum; TA – terminal apophysis; T – tegulum; TM – terminal membrane.

The copulatory organs of *Eocoptarthria echemophthalma* are significantly more complex than the males of other species. Their most important characteristics are: 1) increased complexity in the apical division of the bulb, with a distal sclerotized tube, lateral subterminal and terminal apophyses, and a fulcrum; and 2) a well-developed, species-specific retrolateral tibial apophysis.

Eocoptarthria grisea (L. Koch 1873) (Fig. 6) has basic characteristics similar to *E. echemophthalma*. Its RTA is species-specific and may be used for identification of this spider. The conductor is a broad spoon-shaped inflatable membrane. The median apophysis is long and heavily sclerotized, with a curved and sharp hook at the tip. The apical division of *E. grisea* has the same structures as *E. echemophthalma*. The distal sclerotized tube, embolus, subterminal and terminal apophyses are present. The fulcrum of *E. grisea* is even more complex than that of *E. echemophthalma*. It consists of a set of small sclerites and inflatable membranes. Besides these structures, we have found an additional sclerotized apophysis on the border between the distal sclerotized tube and the tegulum. The sclerite that has a similar position and attachment to other bulb structures in pisaurids Sierwald (1990) is called the "distal apophysis". Authors think that it is reasonable to use this term in describing similar structures in gnaphosid spiders. However, usage of this term does not suppose the homology between them in pisaurid and gnaphosid spiders.

Eocoptarthria penicillata (Simon 1908) (Fig. 7). Figure 7 illustrates the most important bulb structures of *E. penicillata*. The distal apophysis in these spiders is a broad scale-like transparent sclerite at the base of the distal sclerotized tube. It attaches to the tegulum and distal sclerotized tube. This particular sclerite position was considered the distal apophysis by Sierwald (1990). It is difficult to determine whether this structure is homologous to the sclerites in the same position of pisaurid spiders. The apical division of the bulb bears subterminal dentate and spoon-shaped terminal apophyses. The embolus is closely associated with the fulcrum, which supports the tip of the embolus.

DISCUSSION

Analysis of the species mentioned above provides the opportunity to reconstruct the basic ground plan of the spiders studied (Fig. 8) and helps us to draw conclusions about the general organization of the male palps of gnaphosid spiders. As seen in Fig. 8, the ground plan of the gnaphosid palp is tripartite, including three basic sclerites: the subtegulum, tegulum and embolus, bound together by inflatable membranes. The membrane that attaches the subtegulum to the alveolus of the cymbium is a basal hematodocha. The median hematodocha binds the subtegulum and the tegulum. As indicated above, the use of the term distal hematodocha (Comstock 1910, 1920) is avoided because its description and

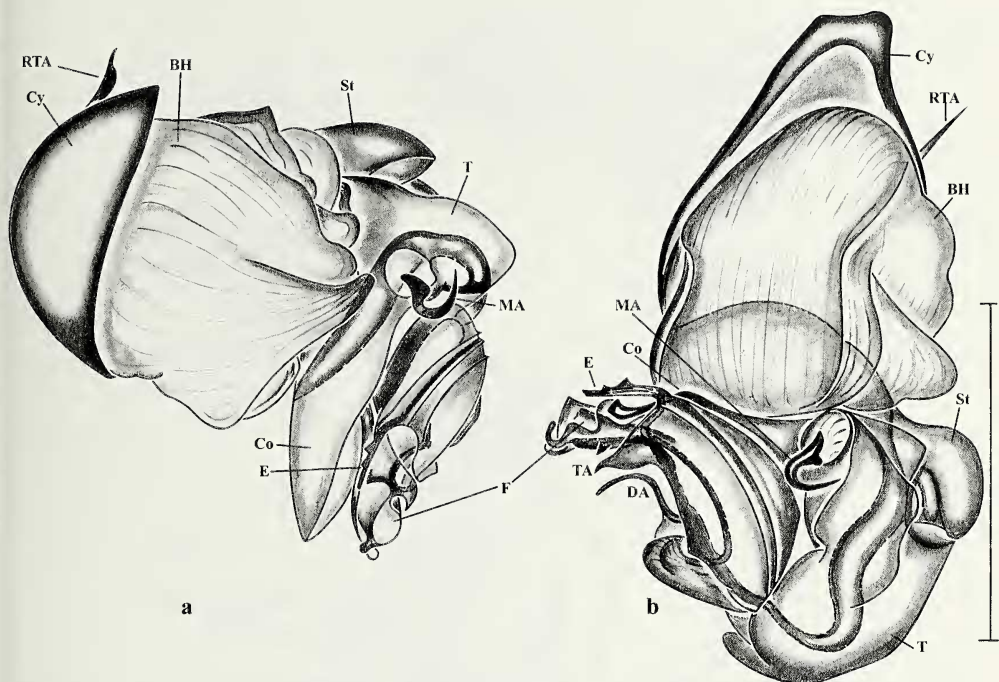


Figure 6.—*Encopitarthria grisea*, left palp. a. Lateral view; b. Ventral view. BH – basal hematodocha; Co – conductor; Cy – cymbium; DA – distal apophysis; E – embolus; F – fulcrum; MA – median apophysis; RTA – retrolateral tibial apophysis; St – subtegulum; T – tegulum; TA – terminal apophysis.

position in the bulb is not clearly identified. Thus, in one case, Comstock identifies the distal haematodocha as an expandable membrane that forms a wall on one side with the radix and stipes on the other side (Comstock 1920:177). In other species its position is between the distal end of the stipes and the embolus and the terminal apophysis (Comstock 1920:179), or between the terminal apophysis and median subterminal apophysis (Comstock 1920:181). Instead, we propose the term “distal tubular membrane” (DTM) to refer to the membrane that connects the distal part of the tegulum with the proximal end of the distal sclerotized tube or embolus and the term “terminal membrane” (TM) to refer to the inflatable membrane associated with embolus. Senglet (2004) uses ‘embolar hematodocha’ to describe the structures of the male bulbs of *Zelotes*, *Drassyllus*, and *Trachyzelotes*. This embolar hematodocha corresponds to the terminal membrane of *Zelanda* and *Encopitarthria*. Murphy (2007) assigned *Zelotes*, *Drassyllus*, and *Trachyzelotes* to the *Zelotes* group, whereas *Zelanda* and *Encopitarthria* belong to the *Echemus* group. Homology between the embolar hematodocha and terminal membrane is questionable and needs further study.

Comparative analysis of palps shows that bulbs of *Encopitarthria* males differ significantly from other gnaphosid spiders by the complex organization of their apical division.

Beside the distal sclerotized tube, they also have a prominent distal apophysis. These are also closely related to the embolus terminal apophysis, fulcrum and terminal membrane. The latter structure was observed only in the sister group *Zelanda*. However, the palp of *Zelanda* has a much simpler organization in general. The terminal apophysis and terminal membrane (or terminal hematodocha) were also observed in *Zelotes* (Senglet 2004). The most simply organized gnaphosid palps are those of *Drassodes* and *Intruda*. Their organization is based completely on the tripartite structure: the subtegulum, tegulum and embolus, which are supported by the conductor and median apophysis. There are no additional visible structures in the palps of these spiders.

The available material on palp ontogeny is scarce and describes only the development of the Salticidae (Wagner 1886; Barrows 1925; Harm 1934), Agelenidae (Szobathy 1915), Theridiidae (Barrows 1925; Bhatnagar & Rempel 1962), Lycosidae (Barrows 1925; Sadana 1971), Linyphiidae (Gassmann 1925) and Segestriidae (Harm 1931). There are no data on male palp ontogeny in gnaphosid spiders. However, some general conclusions may be cautiously applied to gnaphosid spiders as well. As studies show, the male genital bulb originates from the male palp claw fundament, which is responsible for the development of the dorsal claw

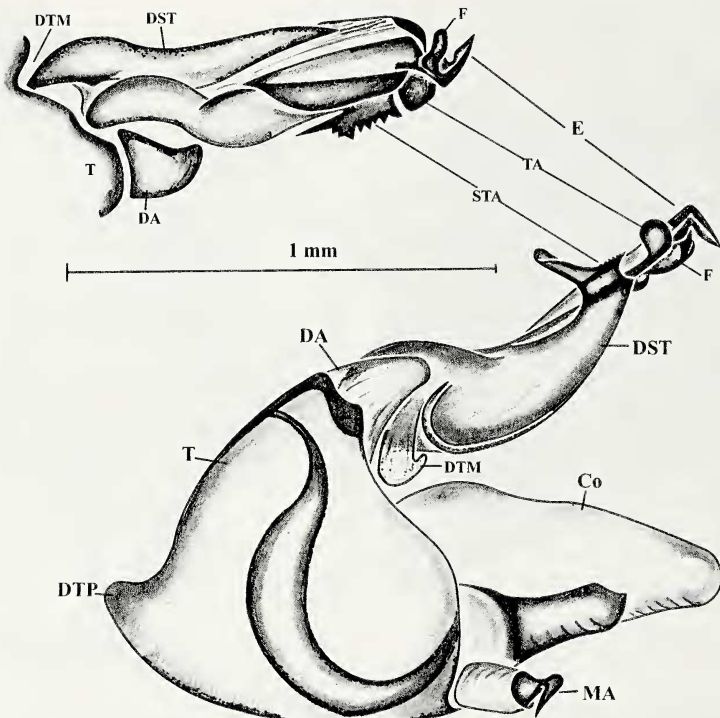


Figure 7.—*Encopitarthria penicillata*, left palp. a. Apical division of the bulb; b. Middle and apical bulb division. Co – conductor; DA – distal apophysis; DST – distal sclerotized tube; DTM – distal tubular membrane; DTP – distal tegular projection; E – embolus; F – fulcrum; MA – median apophysis; PP – pars pendulum of embolus; STA – subterminal apophysis; T – tegulum; TA – terminal apophysis; Tr – truncus of embolus.

extensor and the ventral flexor tendon. At a very early stage, the cell mass of the claw fundament divides into dorsal and ventral parts. The ventral part forms the basal, middle and apical divisions of the bulb, including the sperm duct. The dorsal part gives rise to the conductor and the median apophysis. The ventral cellular mass divides two times. At the first division, the apical division of the palp (embolus) is separated from the still undivided basal and middle divisions. The separation of basal and middle divisions (subtegulum and tegulum) occurs later in ontogeny. There is a strong relationship between the subdivision of the sperm duct and the major sclerites of the bulb. The fundus occupies the position inside the subtegulum. The sperm duct sensu stricto extends through the tegulum. The ejaculatory duct begins as a constriction of the sperm duct on the border between the tegulum (middle bulb division) and apical bulb division and opens at the embolar tip (Fig. 8). On the border between the middle and apical parts of the bulb, the sperm duct narrows into an ejaculatory duct. Thus, this constriction can be used as a criterion for separation of the structures of the middle and apical parts. According to this criterion, the distal sclerotized

tube is a part of the apical division of the bulb, because it lies distal to this constriction. If the tripartite genital bulb in male spiders is a plesiomorphic character (Platnick & Gertsch 1976; Kraus 1978; Haupt 1983; Coddington 1990; Sierwald 1990), then the large sclerites (subtegulum, tegulum and embolus) of all Entelegynae are homologous. In this case, the palp structure of *Zelandia* is the most basal and is structurally similar to that of the common ancestor. Its basic characteristics are a tripartite bulb divided on the subtegulum, tegulum, and embolus and flexibly jointed by inflatable membranes (basal hematodocha, middle hematodocha, and distal tubular membrane). Bulbs of other spiders are derived from this "simple" form. *Encopitarthria* has a more complex organization of the embolar part than that of *Zelandia*. The same tendency of increasing bulb complexity was observed in genera *Zelotes*, *Drassyllus* and *Trachyzelotes* (Miller 1967; Platnick & Shadab 1983; Senglet 2004). All these spiders have an apical division of the bulb that is subdivided into the distal sclerotized tube and the embolus itself. In *Zelotes* Platnick & Shadab (1983) described an intercalated sclerite, which according to our study most likely corresponds to the distal

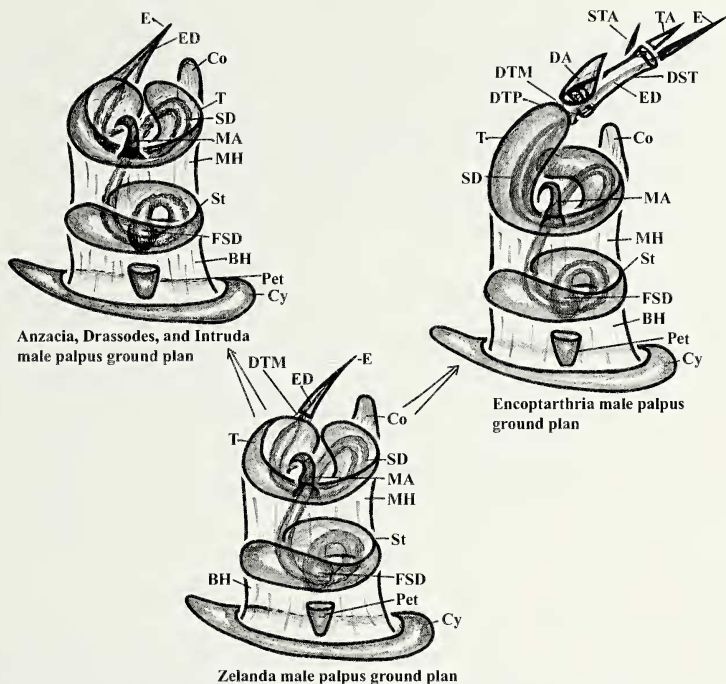


Figure 8.—Ground plan of gnaphosid male palp. BH – basal hematodocha; Co – conductor; Cy – cymbium; DA – distal apophysis; DST – distal sclerotized tube; DTM – distal tubular membrane; DTP – distal tegular projection; E – embolus; ED – ejaculatory duct; FSD – fundus of sperm duct; MA – median apophysis; MH – median hematodocha; Pet – petioles; SD – sperm duct; St – subtegulum; STA – subterminal apophysis; T – tegulum; TA – terminal apophysis.

sclerotized tube of *Encoptarthria*. Both the intercalated sclerite of *Zelotes* and the distal sclerotized tube in *Encoptarthria* are movably connected on one side with the tegulum and on the other side with the embolus. The apical part of the bulb of these spiders also has additional sclerites, such as the subterminal, terminal apophyses and the fulcrum. On the other hand, the male bulbs of *Anzacia*, *Drassodes* and *Intruda* are more simply organized than those of *Zelanda*, *Zelotes*, and *Encoptarthria*. The proximal side of the embolus in *Anzacia*, *Drassodes* and *Intruda* is fused with the distal end of the tegulum. Thus, the embolus in these species is firmly attached to the tegulum, and the distal tubular membrane is absent.

The goal of the present study is to analyze and label the structures of the male genital bulb of *Encoptarthria* spiders as well as the male genital bulbs of the Australian genera *Anzacia*, *Intruda*, and *Zelanda*. The material studied is not sufficient to make evolutionary statements. For a solid evolutionary analysis, further study of the male bulb of other gnaphosid genera and closely related groups is required. Absence of material on gnaphosid palp ontogeny prevents us from making stronger statements on the homology of some structures. However, as studies on male bulb development in other groups show, the cellular mass that gives rise to apical

division separates from the other parts at the first division (Wagner 1886; Szombathy 1915; Barrows 1925; Gassmann 1925; Harm 1931, 1934; Bhatnagar & Rempel 1962; Sadana 1971). Thus, separation of the embolus from other sclerites takes place in the earliest stages of male bulb development and is the plesiomorphic character for the Entelegynae spiders. In this case, the organization of the tripartite bulb is a plesiomorphic state of a gnaphosid bulb. The state where the embolus is firmly attached to the tegulum is most probably a derived condition of male genital bulb organization. One may very cautiously conclude that it most likely represents a general trend in evolution of the male bulb of gnaphosid spiders.

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LITERATURE CITED

- Barrows, W.M. 1925. Modification and development of the arachnid palpal claw with special reference to spiders. *Annals of the Entomological Society of America* 18:383-525.
- Bhatnagar, R.D.S. & J.G. Rempel. 1962. The structure, function, and postembryonic development of the male and female copulatory organs of the black widow spider *Latrodectus curacaviensis* (Muller). *Canadian Journal of Zoology* 40:465-510.
- Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb weaving spiders and their relatives, with comments on phylogeny (Araneocladata: Araneioidea, Deinopoidea). *Smithsonian Contributions to Zoology* 496:1-52.
- Comstock, J.H. 1910. The palpi of male spiders. *Annals of the Entomological Society of America* 3:161-185.
- Comstock, J.H. 1920. *The Spider Book*. Doubleday, Page & Company, Garden City, New York.
- Fedoryak, M., V. Ovtcharenko & B. Zakharov. 2005. Distribution and relations of ground spider genus *Taieria* (Araneae, Gnaphosidae) in Australasia. p. 24. *In* American Arachnological Society, 29th Annual Meeting, 26-30 June 2005, University of Akron, Ohio, USA.
- Foelix, R.F. 1996. *Biology of Spiders*, Second edition. Oxford University Press, Oxford, UK.
- Forster, R.R. 1979. The spiders of New Zealand. Part V. Cycloctenidae, Gnaphosidae, Clubionidae. *Otago Museum Bulletin* 5:1-95.
- Gassmann, F. 1925. Die Entwicklung des männlichen Spinnentasters, dargestellt an *Lephyphantes nebulosus* Sund. *Zeitschrift für Morphologie und Ökologie der Tiere* 5:98-118.
- Harm, M. 1931. Beiträge zur Kenntnis des Baues, der Function und der Entwicklung des akzessorischen Kopulationsorgans von *Segestria bavarica* C.L. Koch. *Zeitschrift für Morphologie und Ökologie der Tiere* 22:629-670.
- Harm, M. 1934. Bau, Funktion, und Entwicklung des akzessorischen Kopulationorgans von *Evarcha marcgravi* Scop. *Zeitschrift für Wissenschaftlichen Zoologie* 146:123-134.
- Haupt, J. 1983. Vergleichende Morphologie der Genitalorgane und Phylogenie der liphistiomorphen Webspinnen (Araneae: Mesotheleae). I: Revision der bisher bekannten Arten. *Zeitschrift für Zoologischen Systematik und Evolutionforschung* 21:275-293.
- Heimer, S. 1982. Interne Arretierungsmechanismen an den kopulationsorganen männlicher Spinnen (Arachnida, Araneae). *Entomologische Abhandlungen* 45:35-64.
- Koch, L. 1873. Die Arachniden Australiens. *Nürnberg* 1:369-472.
- Kraus, O. 1978. *Liphistius* and the evolution of spider genitalia. *Symposium of the Zoological Society of London* 42:235-254.
- Kraus, O. 1984. Male spider genitalia: evolutionary changes in structure and function. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 27:373-382.
- Main, B.Y. 1954. Spiders and Opiliones. *In* The Archipelago of the Recherche. *Australian Geographical Society Reports* 1:37-53.
- Miller, F. 1967. Studien über die Kopulationsorgane der Spinnengattung *Zelotes*, *Micaria*, *Robertus* und *Dipoena* nebst Beschreibung einiger neuen oder unvollkommen bekannten Spinnenarten. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae - Brno* 1:251-298.
- Murphy, J. 2007. Gnaphosid Genera of the World. *British Arachnological Society, St. Neots, Cambridgeshire, UK*.
- Ovtsharenko, V.I., M.M. Fedoryak & B.P. Zakharov. 2006. Ground spiders of the genus *Taieria* Forster, 1979 in New Zealand: taxonomy and distribution (Araneae: Gnaphosidae). *In* *European Arachnology 2005*. (C. Deltshv & P. Stoev, eds.). *Acta Zoologica Bulgarica Supplement* 1:87-94.
- Ovtcharenko, V.I. & B.P. Zakharov. 2006. A peculiar *Encoparthria* group of ground spiders (Araneae, Gnaphosidae) from Australia. p. 30. *In* American Arachnological Society, 30th Annual Meeting, June 2006, Baltimore, Maryland.
- Patterson, C. 1982. Morphological characters and homology. *In* *Problems of Phylogenetic Reconstruction*. (K.A. Joysey & A.E. Friday, eds.). *Systematics Association Special Volume* 21:21-74. Academic Press, London.
- Platnick, N.I. & W.J. Gertsch. 1976. The suborders of spiders: a cladistic analysis (Arachnida, Araneae). *American Museum Novitates* 2607:1-15.
- Platnick, N.I. & M.U. Shadab. 1983. A revision of the American spiders of the genus *Zelotes* (Araneae, Gnaphosidae). *Bulletin of the American Museum of Natural History* 174:97-192.
- Platnick, N.I. 1990. Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosidae). *American Museum Novitates* 2978:1-42.
- Remane, A. 1956. Die Grundlagen des natürlichen Systems der vergleichenden Anatomie und der Phylogenetik. *Geest und Portig, Leipzig*.
- Sadana, G.L. 1971. Studies on the postembryonic development of the palpal organ of *Lycosa chaperi* Simon (Lycosidae: Araneida). *Zoologische Anzeiger* 186:251-258.
- Senglet, A. 2004. Copulatory mechanisms in *Zelotes*, *Drassyllus* and *Trachyzelotes* (Araneae, Gnaphosidae), with additional faunistic and taxonomic data on species from southwest Europe. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 77:87-119.
- Sierwald, P. & J.A. Coddington. 1988. Functional aspects of the male palpal organ in *Dolomedes tenebrosus*, with notes on the mating behavior (Araneae, Pisauridae). *Journal of Arachnology* 16:262-265.
- Sierwald, P. 1990. Morphology and homologous features in the male palpal organ in Pisauridae and other spider families, with notes on the taxonomy of Pisauridae (Arachnida: Araneae). *Nemouria* 35:1-59.
- Simon, E. 1908. Araneae. Ire partie. *In* Die Fauna Südwest-Australiens 1(12):359-446. *Michaelsen & Hartmeyer, Jena*.
- Szombathy, K. 1915. Über Bau und Funktion des Bulbus der männlichen Kopulationsorgane bei *Agelena* und *Mygale*. *Annales Historico-naturales Musei Nationalis Hungarici* 13:252-276.
- Wagner, W. 1886. Development and morphology of copulation organs in Araneae. *Izvestia Imperatorskago Obchiestwa Lioubitelei Iestiestvoznania, Antropology i Etnografy, Sostoiaschago pri Imperatorskom Moskovskom Universitete (Moscow)* 50:200-236.
- Wagner, W. 1887. Copulationsorgane des Männchens als Criterium für die Systematik der Spinnen. *Horae Societas Entomologicae Rossicae* 22:3-132.

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